

THE GENUS *PARANAIS* (OLIGOCHAETA: NAIDIDAE) IN NORTH AMERICA

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Abstract.—Nephridia have been found in some specimens of three *Paranaïs* species. These vary in degree of development from rudimentary structures to fully formed but closed nephridia, all within each species. Because the genus *Wapsa* is identical to *Paranaïs* apart from the supposed absence of nephridia in the latter, we now regard *Wapsa* as a synonym of *Paranaïs*. *Paranaïs birsteini* Sokolskaya is reported from the Pacific Northwest, bringing the total number of *Paranaïs* species in North America to four. *Wapsa grandis* Harman is transferred to *Paranaïs*; *Paranaïs frici* Hrabé is confirmed as a North American species with *Wapsa mobilis* Liang as a probable synonym. The type-species, *Paranaïs litoralis* (Müller) is widely distributed in North America.

While *Paranaïs litoralis* (Müller) has been recognised as part of the North American fauna since 1905 (Moore 1915), it was not until much later that the second species, *Paranaïs frici* Hrabé was identified in the San Francisco Bay area (Brinkhurst and Simmons 1968). The latter is now recognised as a North American species by its original describer (Hrabé 1981).

The genus *Wapsa* was erected by Marcus (1965) for a single Brazilian species, *W. evelinae*, the new genus being separable from *Paranaïs* by the presence of nephridia. Brinkhurst (1971) transferred the Chinese species *Paranaïs mobilis* Liang to *Wapsa* because it shared the nephridial character with the type-species, and both species have papillate body walls. Harman (1977) described *Wapsa grandis* based on differences between this species (from Louisiana) and the two existing *Wapsa* species, but relied on the papillate nature of the body wall for the separation from *Paranaïs* species. Hiltunen and Klemm (1980) preferred to recognise other papillate North American material (with setae that differ from those of *W. grandis*) as *W. mobilis* rather than *P. frici*, a position not supported by Brinkhurst and Kathman (1983). The separation of the genus *Wapsa* from *Paranaïs* can no longer be maintained because it is shown here that nephridia may be present in all of these species, and that there may be at least some accumulation of foreign material, with or without papillae, on the body wall in all of them. This, coupled with the discovery of a fourth North American taxon in a large collection of fully mature specimens from many parts of the world, has prompted this revision of the genus *Paranaïs* with special reference to the North American forms.

Methods

This study was based on examination of stained whole mounted specimens of all four North American species in Canada Balsam, sectioned material of *P. litoralis* and *P. frici*, and some unstained whole mounted material, all from a variety of sources noted under each specific account. Mature specimens were used

throughout. A much larger collection of immature specimens from Western Europe and North America was not used even though all four species can now be recognised on the basis of somatic characters alone, and two species have a limited distribution.

The type-specimens of *P. botniensis* from the Swedish Museum of Natural History were examined for us by C. Erséus.

Not all of those characteristics that were measured (setal lengths, widths and lengths of atria and spermathecae, thickness of the walls of those organs) could be discerned on every specimen, so that the number of measurements reported in Table 1 and Fig. 4 is less than the number of mature specimens available. Hotelling's T^2 statistic (generalised t statistic) was used to test for a significant difference between the mean lengths and widths of the atria in *P. litoralis* and *P. birsteini*.

Since complete synonymies were reported by Brinkhurst (1971), only those citations published subsequent to that account are documented here.

Paranais Cerniavsky, 1880

No eyes. Setae all of one shape, starting in V dorsally, II ventrally. Ventral setae of II often slightly longer than rest, and somewhat more lateral in position. Glandular pharyngeal pouch in III, pharyngeal glands in IV. Nephridia closed, or absent, variable within a species. Coelomocytes present. Spermathecae and testes in IV, ovaries and atria in V, no prostates on either atria or vasa deferentia. Penial setae slightly or fully modified. Body wall often with covering of foreign matter, sometimes with papillae. Cosmopolitan.

Type-species.—*Nais litoralis* Muller.

Remarks.—The discovery of nephridial tissue in all four North American species of *Paranais* (Fig. 1 illustrates this for two of the species) makes the retention of the genus *Wapsa* Marcus, 1965 unnecessary. As a result, some species of *Wapsa* prove to be synonymous with *Paranais* species as detailed below.

Paranais litoralis (Muller, 1784)

Figs. 1–4, Table 1

Paranais litoralis (Muller), subspecies *orientalis* Sokolskaya, 1964:57, fig. 1.

Diagnosis.— $l = 9$ – 14 mm (living), $s = 13$ – 46 . Ventral setae of II mostly 5, from 4–7 per bundle, slightly longer than rest (Table 1) with upper teeth distinctly longer than lower. Ventral setae of III–IV mostly 3, sometimes 4 per bundle, with upper teeth nearly equal in length to lower, in median and posterior bundles usually 3, ranging from 2–4, with upper teeth varying from slightly longer to slightly shorter than lower. Penial setae from 3–6 or even 7 per bundle with long, straight, proximal ends and short, strongly curved, distal ends terminating in small bifid tips. Dorsal setae from V, 2–4, mostly 3 per bundle, all with teeth approximately equal in length. Spermathecal ampullae and atria long, 2–5 times longer than broad (average 3.04, $n = 42$, $s = 0.71$) atria with muscle layers from 2– $18\ \mu\text{m}$ thick. Spermathecal and atrial ducts distinct but varying in length. Spermathecal pores lie well ahead of and below setal line in IV. Body wall exhibits deep transverse folds (preserved material) with thin layer of attached foreign

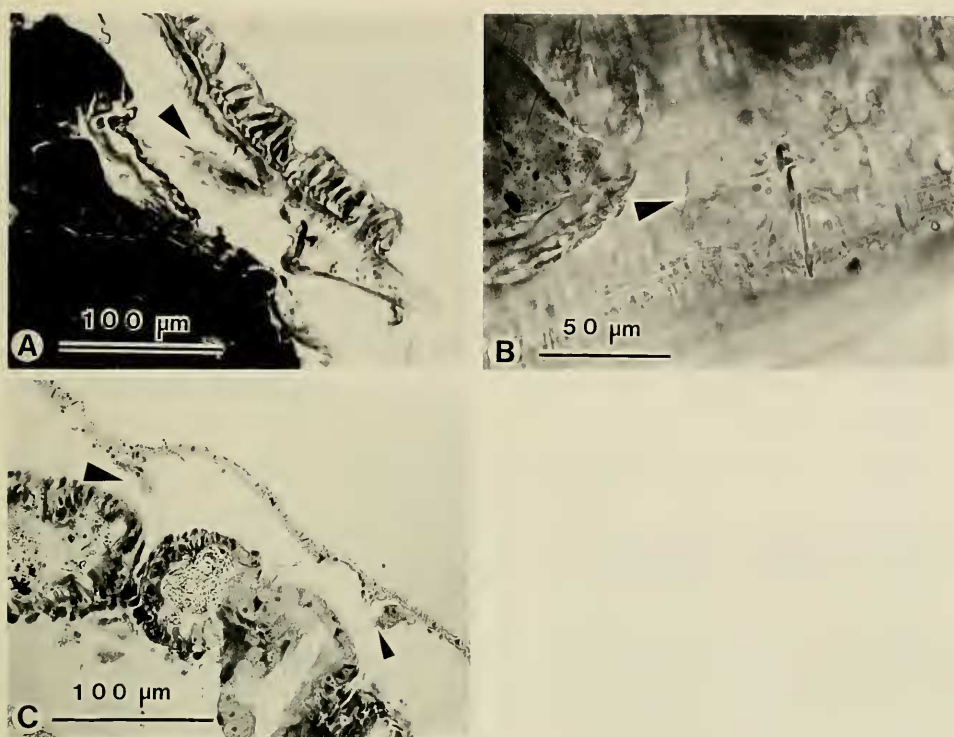


Fig. 1. Nephridial tissue: A, B, *Paranais litoralis*; C, *P. frici*.

material in some specimens. Cosmopolitan. Salt or brackish water, inland as well as coastal.

Remarks.—This description is based on examination of 50 mature specimens from North America, Europe, Australia, and Hong Kong. The lengths and breadths of the atria, a feature of importance in the separation of this species from another North American species, *P. birsteini*, are plotted in Fig. 4 for material from five geographic areas. Considerable overlap in the ratios is demonstrated between these five sets of *P. litoralis* material, but when considered as a single set, *P. litoralis* is significantly different to *P. birsteini* (P value less than 0.005). This can largely be attributed to differences in length. Care should be exercised in the application of these measurements, because partially mature or even mature but unmated individuals of *P. litoralis* can yield small values that fall within the range observed for *P. birsteini*. While the length/breadth ratios for spermathecae and atria vary (Europe 2.7, Atlantic North America 2.7, Pacific Canada 2.6, Australia 3.4), we feel that the large degree of overlap observed precludes the recognition of subspecies, such as that erected by Sokolskaya (1964).

This species is common and abundant in so many saline habitats that a listing of those sites from which specimens were obtained in western Europe and North America is unnecessary. Two collections should be mentioned, which are material from Hong Kong (Deep Bay and Tolo Harbour, New Territories, coll. C. Erséus) and Australia (Fraser Island, Gippsland Lakes and Port Phillip Bay, Victoria, G. C. B. Poore, deposited National Museum of Victoria, Melbourne, Australia).

Table 1.—Setal lengths of *Paranaïs* species, expressed as mean $\mu\text{m}(s/\sqrt{n})$. n is a maximum figure, in some instances fewer measures were available.

Setae from:	II	III/IV	Penial	After VI	n
<i>P. littoralis</i>					
Pacific Canada	87 (5)	72 (2)	87 (5)	75 (3)	16
Australia	69 (4)	66 (4)	54 (4)	60 (4)	11
Europe	96 (3)	78 (3)	90 (4)	78 (3)	14
All specimens	77 (3)	72 (2)	78 (4)	72 (2)	41
<i>P. birsteini</i>	69 (2)	66 (2)	66 (2)	66 (2)	30
<i>P. frici</i>	99 (6)	87 (4)	90 (4)	93 (4)	15
<i>P. grandis</i>	136 (4)	96 (5)	105 (15)	119 (9)	8

Paranaïs frici Hrabe, 1941

Figs. 1–3, Table 1

Paranaïs frici Hrabe, Finogenova, 1972:114, figs. 51–53.

Wapsa mobilis Liang, Hiltunen and Klemm, 1980.

Diagnosis.— $l = 9$ mm (living), $s = 13$ –42. Ventral setae of II 2–4 per bundle, upper tooth at least twice as long as lower. In all other bundles apart from ventrals of V, 1–2, rarely 3, setae per bundle, all with upper teeth distinctly longer than lower. Penial setae in V thicker than rest, with short distal ends, clearly bifid, 2–3 per bundle. Mean lengths of setae are presented in Table 1. Spermathecal and atrial ampullae small, globular, and having very thin muscle layers. Spermathecal and atrial ducts distinct but variable in length, up to twice as long as broad. Spermathecal pores varying in position from well in front of the ventral setae to beside them in IV. Body wall with transverse furrows and thin layer of foreign matter. Fresh and brackish water, Europe, North America, Africa, possibly South America (see below).

Material examined.—Upper Newport Bay, California, Jun 1978, M. Quammen; San Francisco Bay area, 1961/62, see Brinkhurst and Simmons 1968; Fraser River, British Columbia, see Brinkhurst 1978; Lake St. Claire, Michigan, May 1979, coll. et det. J. Hiltunen.

Remarks.—The setae of this species are distinctive, especially the shape of the upper tooth relative to the lower and its length in postclitellar bundles. This setal form is shared by *P. grandis* (see below), but in that species the setae are both more abundant and much larger (Table 1) and the penial setae are more strongly modified than in the former. Sperber (1948) stated that the setae of *P. frici* reached $105 \mu\text{m}$ in II, the others being a little shorter. Sokolskaya says they reach a maximum of $106 \mu\text{m}$ but are all similar in length, but Laakso (1969) quotes a maximum of $139 \mu\text{m}$ in II reducing to at least $105 \mu\text{m}$ posteriorly.

In the original accounts of both *P. frici* and *P. simplex*, Hrabe (1936, 1941) referred to the penial setae as being shaped like ordinary ventrals (according to translations from Russian and Czech). We take this to mean that they are sigmoid, as in other ventral setae, which indeed they are. They are modified, however, as they are thicker than usual, and they have shortened distal ends (Fig. 2). The

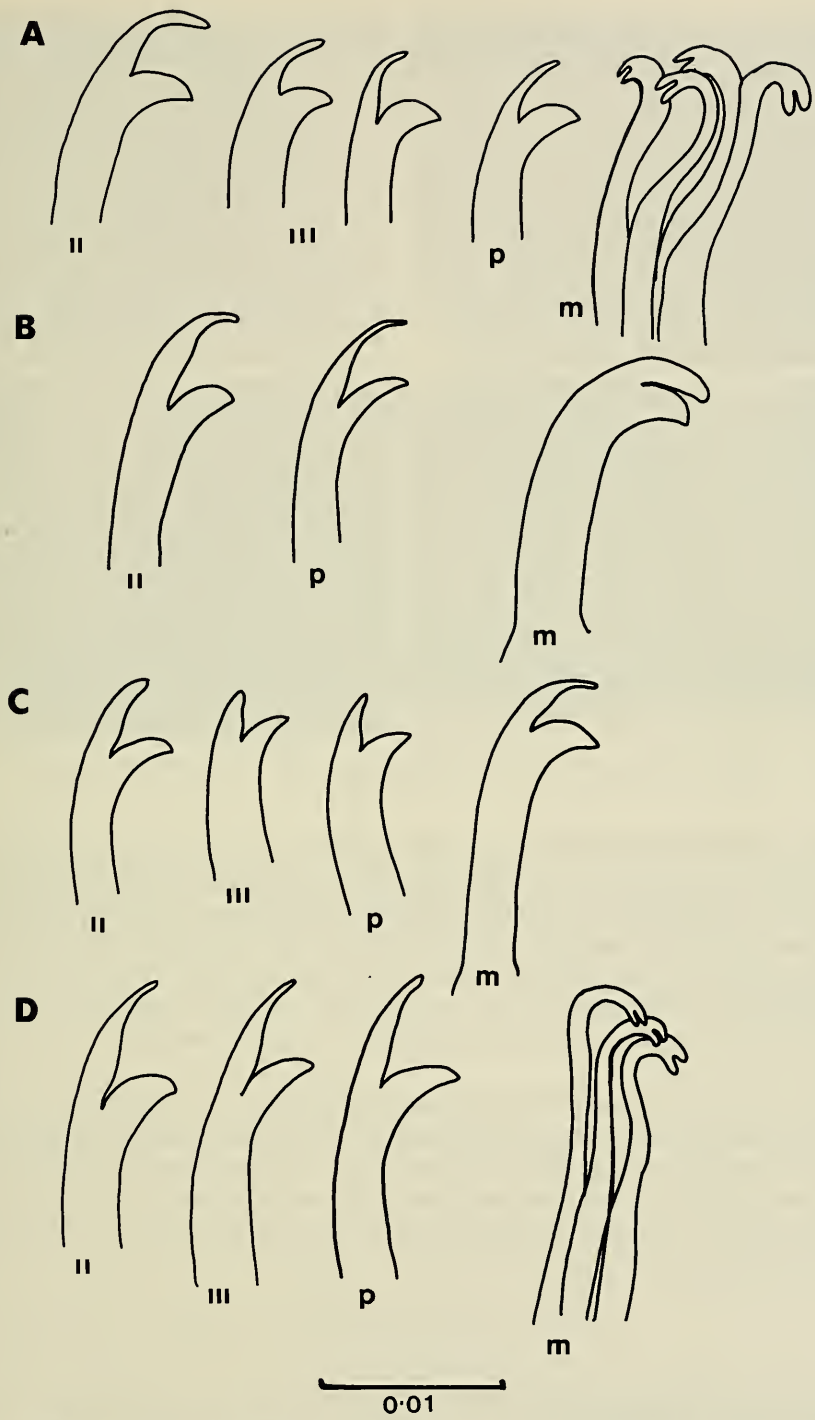


Fig. 2. Setae of *Paranais* species: A, *P. litoralis*; B, *P. frici*; C, *P. birsteini*; D, *P. grandis*. II, III, ventral setae of segments II, III; p, posterior setae; m, penial setae.

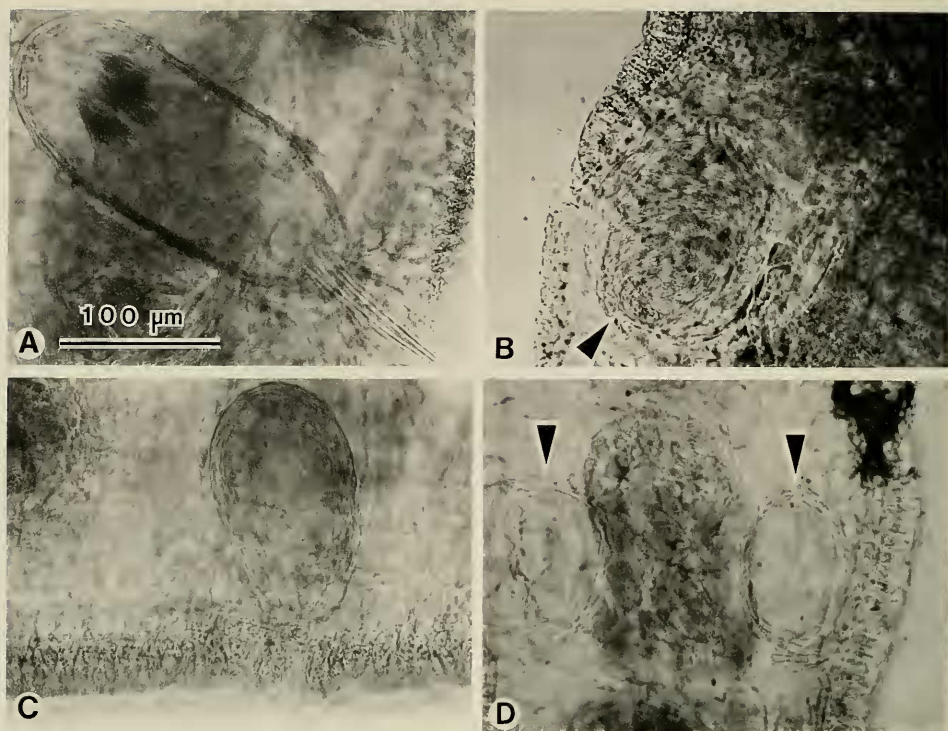


Fig. 3. Atria of *Paranaïs* species: A, *P. litoralis*; B, *P. frici*; C, *P. birsteini*; D, *P. grandis*.

distal ends are bifid, but the teeth are short and equally long in contrast to other ventrals. In this respect the description of the penial setae by Liang (1958, translated from Chinese) at least acknowledges these differences by identifying them as genital setae. It is primarily because definite penial setae can be observed in North American material that Hiltunen and Klemm (1980) changed the original identification of this species from *P. frici* to *W. mobilis*. The genital setae illustrated by Brinkhurst (1978) are attributable to a specimen of *P. litoralis* found among some *P. frici*.

Because several of our specimens have nephridia, there do not seem to be any substantial differences between *P. frici* and *W. mobilis*, as discussed by Sokolskaya (1971). According to that account, both species have similar atria with walls $8\text{ }\mu\text{m}$ thick, the other dimensions being $84 \times 67\text{ }\mu\text{m}$ versus $82 \times 70\text{ }\mu\text{m}$. The body wall of *P. frici* is now acknowledged to be covered in foreign matter according to all recent accounts (see Hrabe 1981, for example).

Paranaïs birsteini Sokolskaya, 1971

Figs. 2–4, Table 1

Paranaïs birsteini Sokolskaya, 1971:930, figs. 1–6.

Diagnosis.— $l = 3.5\text{--}5.0\text{ mm}$, $s = 21\text{--}42$. Ventral setae of II 5–7, with upper teeth twice length of lower. Ventral setae of III–IV 4–5 per bundle with upper teeth longer than lower, reduced to 2–4 behind the clitellum, where teeth are

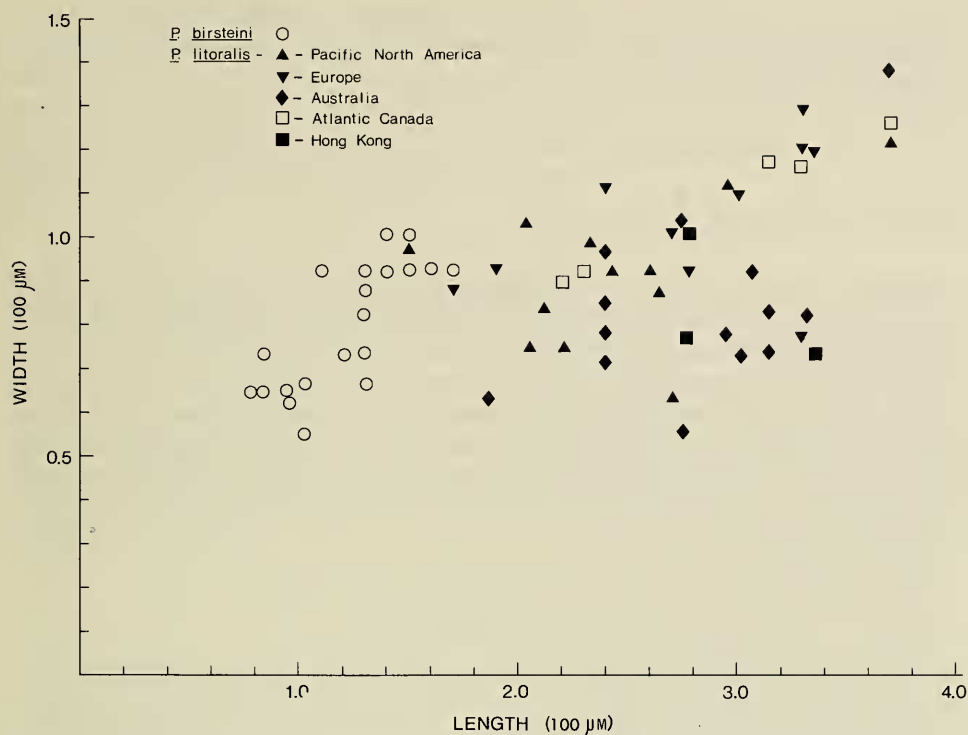


Fig. 4. Dimensions of atria of *Paranais litoralis* and *P. birsteini*.

nearly equal in length. Penial setae in V paired in each bundle, with short distal ends and short teeth of equal length. Dorsal setae 3–4, rarely 5 in V, 2–4 in rest of dorsal bundles. Spermathecal and atrial ampullae ovoid, atrial length to breadth ratio 1.2–1.9 ($\bar{x} = 1.5$, $n = 19$, $s = 0.19$), atrial ampullae with thick muscular walls. Spermathecal and atrial ducts distinct, spermathecal pores vary in position from in front of and below or adjacent to ventral setae. Body wall distinctly papillate, with transverse ridges with foreign material in grooves. Kamchatka, USSR, and Pacific coast of Canada.

Material examined.—19 mature specimens, from: Wainwright Basin, Tsimpsean Peninsula below Prince Rupert; Tomahawk Island, Nowlan Passage; Horkarson Point and Ram Bluff, Dean Channel, Rattenbury Point, Fisher Channel, near Ocean Falls; Mowitch Point and Ecstall River confluence with Skeena River, Skeena River estuary; Alberni Inlet, Tahsish Inlet, Moyeha Bay, Sydney Inlet, Vancouver Island, all British Columbia, coll. H. R. Baker and K. A. Coates, 1979–1981. Skagit River Flats, mouth of the north fork, Skagit River, Washington coll. E. Gallagher, Dec 1979.

Remarks.—The new material from British Columbia and Washington is remarkably similar to that described from Kamchatka, and it would be reasonable to assume that this is a Pacific Rim species. The atrial walls in the original material are said to be 17 μm thick; here they vary from 9 to 24 μm with a mean of 17 μm . The length/breadth ratio of the atria of the original is 1.7, that of the new material is 1.5 (see Fig. 4). The species combines the somatic setae and muscular

atrial walls of the form seen in *P. litoralis* with penial setae like those of *P. frici*. The length and breadth of the atria and spermathecae are intermediate between those of *P. litoralis* and *P. frici*.

Paranais grandis (Harman, 1977), new combination
Figs. 2–3, Table 1

Wapsa grandis Harman, 1977:83, fig. 1.

Diagnosis.—3.0–4.0 mm, s = 28 plus (all fragments). Ventral setae of II 6–7, longer than other setae (105–150 μ m versus 80–122 μ m) with upper teeth much longer than lower. Ventral setae of III–IV 3 per bundle, with similar teeth, ventral setae of V 4, strongly modified penial setae with short, thin, recurved distal ends (88–140 μ m long). Most other ventral bundles with 3 setae, all with long upper teeth. Dorsal setae 2–3 per bundle, similar to rest in form. Spermathecal and atrial ampullae ovoid, length to breadth ratios of 1.3 and 1.4 respectively, with walls thin when fully distended (5 μ m). Body wall papillate with foreign matter attached. Louisiana, Texas, U.S.A.

Material examined.—13 whole-mounted specimens, Sea Rim State Park, Texas, 29 Jan, 1979, coll. J. Wern, det. M. Loden.

Remarks.—Harman (1977) cited the setal lengths in this species as 128–148 μ m in II, 98–106 μ m in III, 109–121 μ m in other ventrals, and a total range of 74–123 μ m for dorsals, the anterior setae being longer than the more posterior setae. He compared these with setal lengths for other *Wapsa* species (*W. mobilis*, *W. evelinae*) and showed that those of *W. grandis* were distinctly longer than those of the other two species. He did not compare the setae with those of *Paranais* species. The setal measurements based on mature specimens of the four species available to us confirm the fact that there is a much greater difference between the setae of II and the other bundles in *P. grandis* than in the other species (Table 1), and that the setae are generally longer overall. Otherwise this species differs from *P. frici* primarily by the possession of fully developed penial setae of the form observed in *P. litoralis*, and by the larger number of somatic and penial setae (Fig. 2).

Other Species

Only one of the following species has been examined, the type-specimens of *P. botniensis* having been studied for us by C. Erséus. Type-material is not available for eastern European species, and the South American species were described from immature specimens.

Paranais simplex Hrabe, 1936

Paranais simplex Hrabe, Kasprzak, 1977:93, figs. 1–4, plates 1–5.

This Ponto-Caspian species has 5–6 ventral setae in II with the teeth equally long, and 3–4 in other bundles with the upper teeth shorter than the lower. The penial setae are paired, sigmoid and bifid. The reproductive system, described by Kasprzak (1977), includes ovoid spermathecae and atria, the latter with thick muscular walls. No dimensions were given in this description, but the illustration

shows the atrial muscles to be about 15 μm thick. This species is very similar to *P. birsteini* apart from the form of the setal teeth. Because of the limited distribution and freshwater habitat, recognition of this as a separate species causes no practical problems, and so unless the setal form can be shown to be the result of the ambient salinity by experimentation, the question of synonymy of *P. birsteini* with this species will not be pursued.

Paranais botniensis Sperber, 1948

This species shares the small setal number and thin muscle layer of the atrial ampulla (2–7 μm) with *P. frici*, but the length/breadth ratio of the atria approaches that of *P. birsteini* (64 by 48 μm , or 76 by 37 in another specimen) as does the form of the setae. The penial setae are paired and bifid, sigmoid as in both of the above. This species has not, to our knowledge, been found outside the brackish water type-locality in Sweden. The setal numbers together with other differences noted by Sperber, strongly suggest that this be regarded as a distinct species. In any case, it does not appear to be a geographic race of *P. litoralis*, one possibility suggested by Sperber.

Paranais macrochaeta Cernosvitov, 1939 and *Paranais salina*
Cernosvitov, 1939

These two species were recorded from saline water in the Lake Titicaca basin, Peru, described from very few immature specimens. The principal difference between these and existing taxa was claimed to be the lateral position of the ventral setae of II relative to those of other bundles, a suggestion maintained by Sokolskaya (1971) in her key to the species in the genus. In all of the species examined by us the setae of II seem to be in this position. The number of setae in *P. macrochaeta* (8–9 in II, 4–5 in all others bar III–IV) is much higher than in *P. frici*, which shares the pattern of setal teeth, with the upper teeth always much longer than the lower. *Paranais salina* resembles *P. litoralis*, but mention of the anus opening into a rectangular fossa-raises doubts. Until mature specimens are collected, these species must remain dubious taxa.

Paranais mobilis Liang, 1958

As nephridia and foreign matter on the body wall have now been discovered in *P. frici*, and the question of the form of the penial setae has been resolved (see above), this species is here regarded as synonymous with *P. frici* (q.v.).

Wapsa evelinae Marcus, 1965

The primary reason for the erection of this species as the type of a new genus was the presence of nephridia. Marcus (1965) did compare the species briefly with the existing *Paranais* species other than *P. mobilis*. The species clearly differs from *P. litoralis* in that the penial setae are sigmoid and bifid, and the atria and spermathecae are globular to ovoid in shape. The muscular layer of the atrial wall is said to be thick, but no measurements are presented and the illustration suggests that they are thinner than those of *P. birsteini* (for example). It is clear that there was considerable variation in setal number and form in the material described

by Marcus (ventrals of II 3–4 or 5–6, in III–IV 2 or 3–4, the upper teeth twice as long as the lower, or less than twice as long). The specimens with the smaller setal number distinctly resemble *P. frici* in both number and form of the setae.

Marcus interpreted literally the statement by Hrabe (1941) regarding the penial setae resembling the other ventral setae, and supposed the slightly modified penial setae of his specimens to be a distinguishing characteristic. He also quotes the presence of intracellular stomach canals in the new species, a character utilised by Sperber (1948). However, in view of our experience with nephridia, and in view of the level of distinction applied to the separation of species throughout the family, we do not feel that this is a sound character, and would not use a single residual character to maintain a distinct species in the absence of other differences.

Some part, at least, of the Marcus material would seem to be attributable to *P. frici* depending on the reliability of observations on the thickness of the muscle layer of the atrial walls. Otherwise some, or even all, of the material closely resembles *P. botniensis* although no mention of papillation of the body wall appears in the original description of that species. This species cannot be identified for certain.

Paranaïs multisetosa Finogenova, 1972

Paranaïs multisetosa Finogenova, 1972:94, figs. 1–5.

In this species there are 8–10 setae in II, with the teeth of equal length. In other ventral bundles there are 3–6, and 3–4 in dorsal bundles. The penial setae number 3–4 and are said to resemble the ventrals (see discussion above). The setal lengths are 62–73 μm (anterior ventrals), 59–64 μm (posterior ventrals), and 61–68 μm (dorsals). The atrial ampullae are 112–117 μm long by 50–75 μm wide, the spermathecae are 70–129 μm long by 36 μm wide, with a long duct. The species is restricted to the Dnieper Bug Firth, in the Black Sea, salinity 0.14–5.6 parts per thousand.

The species is close to *P. simplex*, the Ponto-Caspian species, but has more setae of a shorter length.

Paranaïs palustris Udaltsov, 1907

This species was tentatively attributed to *Homochaeta setosa* (Moszynski, 1933) by Marcus, 1965, but the available descriptions do not justify such an action, so that it is in the interest of stability to regard this species as a dubious taxon. Access to the type, even if one exists, is not feasible. Other *Homochaeta* species have been identified as *Paranaïs* species at various times (see Brinkhurst 1971).

Acknowledgments

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loaned to him has been used extensively in this study. Sections were prepared by the Laboratory of Analytical Systematics of the Royal Ontario Museum.

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Note added in proof: Since this MSS. was prepared, two reports published by N. P. Finogenova have become available and have been translated. *Paranais tjupensis*, described from Issyk-kul Lake, is similar to *P. botniensis* (1977, Hydrobiological studies on the Tyup River and of Tyup Bay on Lake Issyk-kul. Collection of Scientific Papers; U.S.S.R. Academy of Sciences. Leningrad, Zoological Institute). In 1982 the subspecies *orientalis* was promoted to specific rank, though it is very similar to *P. litoralis* and within the range of variation of that species as defined here (Marine Invertebrates of coastal biocenoses of the Arctic Ocean and the Pacific Ocean. Explorations of the fauna of the seas; Academy of Sciences of the U.S.S.R., Zoological Institute).